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## **Intra-seasonal temporal variation of reproductive effort for male grey seals**

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## Abstract

Reproductive skew in polygynous mating systems leads to variation in the mating strategies, or the tactics within strategies, adopted by individual males. For example, variation in the timing of reproductive effort might reflect trade-offs between maximizing access to receptive females and minimizing interactions with competitors. For capital breeding grey seals (*Halichoerus grypus*), male mating success has been positively linked to total duration of tenure, but without differentiation of intra-seasonal changes in reproductive effort. The aims of this study were to identify tactics within the Tenured male strategy based on the timing of social dominance as a metric of reproductive effort, and to compare mating success across identified tactics. Our results confirm that duration of stay on the colony explained the most variation in mating success, but effect strength was reduced for tenures longer than 10 days. Additionally, there was evidence that timing of reproductive effort within a breeding season also contributed to observed variation in mating success. Males that maximized their dominance score at or after the peak in female attendance achieved greater mating success, relative to those who were dominant earlier in the breeding season. Males who timed their reproductive effort earlier in the season still achieved some mating success, but it was reduced. Individuals' tactics were flexible across years, and we found no evidence to support the hypotheses that timing of reproductive effort before or after the peak in female attendance was utilized by smaller Tenured males, or to avoid conflict. These results highlight that understanding temporal scheduling of individual reproductive effort within a breeding season, relative to the availability of resources, constraints of fasting, and intra-male competition, is a key aspect to consider when differentiating individual tactics in long-lived, capital, polygynous breeders.

## Highlights

- Tenured male grey seals' dominance scores shift throughout the breeding season
- Date of peak dominance was used as a proxy for timing of reproductive effort (RE)
- Prolonged length of stay increased mating success non-linearly
- Timing peak RE at or after peak female attendance also increased mating success.
- Tenured male grey seals were flexible in their mating tactics across years

**Keywords:** mating tactics, grey seals, reproductive effort, dominance

## **Introduction**

Mating patterns arise as a function of the spatial and temporal distribution of the limiting sex and the ability to monopolize mating opportunities (Emlen and Oring 1977). In polygynous mating systems, due to the increased conflict and competition for access to females, males often have exaggerated characteristics such as size (Jarman 1983, Carlini et al. 2006, Crocker et al. 2012), ornamentation (Brodsky 1988, Sneddon et al. 1997) or behavioural displays (Clutton-Brock and Albon 1979, Sanvito et al. 2006) that enhance individual fitness. The high reproductive skew in these systems also selects for variation in the mating strategies adopted by individual males (Smith 1982, Gross 1996, Shuster and Wade 2003, Lifjeld et al. 2011, Lidgard et al. 2012).

In spatially and temporally discrete breeding systems, length of stay has been positively correlated with male reproductive success, and so the evolutionary stable strategy is generally agreed to be ‘come early, stay long’ (Smith and Price 1973, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2005, Nagy et al. 2012). Males adopting this strategy are typically referred to as ‘dominant’ or ‘Tenured’ and gain the highest reproductive success (Boness and James 1979, Ellis 1995). Alternatively, peripheral or ‘Transient’ males unable to hold territories or maintain access to females may engage in scramble competition. In these cases, mating opportunities are gained through opportunistic sneaky copulations, or intercepting females (Sandell and Liberg 1992, Lidgard et al. 2004, Huffard et al. 2008, Franco-Trecu et al. 2014, Meise et al. 2014).

Across both of these strategies, timing of arrival and reproductive effort for polygynous males can have implications for mating success (Clutton-Brock et al. 1979, Hoffman et al. 2003, Meise et al. 2014). Early arrival for males is often associated with long tenure and increased mating success (Twiss 1991, Arnould and Duck 1997). Late arrival can result in reduced mating opportunities if fewer sexually receptive females remain (Parker and Maniscalco 2014), or it can reduce costs by targeting periods when male-male competition is less intense (Mason et al. 2012). For example, peak reproductive effort for prime-aged male red deer (*Cervus elaphus*) coincides with female oestrus, and while younger males are present throughout the season, they peak in reproductive effort later (Mysterud et al. 2008). Young male alpine chamois (*Rupicapra rupicapra*) also exhibit greater reproductive effort in the later part of

the breeding season, presumably when competition with dominant, older males is reduced (Mason et al. 2012).

The mating patterns of many pinniped species are characterized by moderate to extreme polygyny and spatially and temporally discrete breeding seasons (Bartholomew 1970, Fitzpatrick et al. 2012, González-Suárez and Cassini 2014). Across most pinniped species, Tenured males that are larger and more dominant tend to stay for longer periods of time, and the duration of an individuals' length of stay within a breeding season shares a strong positive relationship with mating success (Anderson and Fedak 1985, Twiss 1991, Arnould and Duck 1997, Lidgard et al. 2004, Carlini et al. 2006, Pörschmann et al. 2010, Crocker et al. 2012, Lidgard et al. 2012, Franco-Trecu et al. 2014, Meise et al. 2014, Parker and Maniscalco 2014). However, variation of alternative mating tactics within the Tenured strategy, particularly with regard to timing of reproductive effort relative to female abundance, is less well-understood. Studies often generalise timing of reproductive effort to pre- or peak-reproductive periods, based on arrival (Meise et al. 2014) or implicitly assume within-individual reproductive behaviours are uniform over-time and could be averaged across the breeding season (Twiss 1991, Twiss et al. 2006, Lidgard et al. 2004, Franco-Trecu et al. 2014, Parker and Maniscalco 2014).

The tendency to select a coarse resolution for these investigations may be due to logistical difficulties associated with quantifying within-individual and within-season variation in reproductive effort. For example, mass loss is a common proxy for reproductive effort in ungulate studies (Mason et al. 2012) and in studies of capital breeding pinnipeds (Anderson and Fedak 1985, Pomeroy et al. 1999b); but such measures are typically calculated from one early capture and one late capture (Crocker et al. 2012), or at most using 3-4 captures throughout the season (Twiss 1991). This approach provides gross seasonal changes, but is intrusive, and provides limited insight into continuous within-season variability in reproductive effort. Quantifying changes in individual reproductive effort within a breeding season might be approached using behavioural metrics that can be collected at a fine temporal resolution. One such metric is dominance. Highly dominant Tenured male pinnipeds tend to have higher energetic expenditures suggesting dominance can be a proxy for reproductive effort (Twiss 1991, Crocker et al. 2012). Additionally, dominance status relative to others on the colony is not uniform throughout an individuals' tenure (Bishop et al. 2015b), and modern dominance-score calculation techniques such as

Elo scores (Neumann et al. 2011) that follow the sequence of outcomes of aggressive interactions for individuals across time, can track these changes in social dominance at a daily temporal scale within a breeding season. Being able to describe this variation in the scheduling and expression of dominance within a season could therefore be a useful proxy for intra-seasonal variation in reproductive effort.

Grey seals (*Halichoerus grypus*) are an ideal study species to investigate the intra-seasonal variation in timing of male reproductive effort. Grey seal breeding colonies form annually, typically at remote offshore island sites, when females aggregate on shore to give birth to and nurse a single pup, then mate with a male before weaning their pup and returning to sea (Boness and James 1979, Pomeroy et al. 1999, Twiss et al. 2006). Traditionally, individual grey seal males are broadly classified into two strategies: Tenured (present on the breeding colony for  $\geq 2$  consecutive days and involved in  $\geq 10$  male-male aggressive interactions) or Transient (present for  $< 2$  consecutive days; Boness and James 1979, Boness 1984, Anderson and Fedak 1985, Twiss 1991). The Transient strategy is sometimes adopted by younger males until a size/age threshold is met for Tenure (Twiss 1991, Lidgard et al. 2012), and several different tactics within the Transient strategy have been described including: sneaking copulations, failed attempts at Tenured strategies, and aquatic mating (Worthington Wilmer et al. 1999, Lidgard et al. 2001, 2004, 2005, Twiss et al. 2006).

Although length of stay is positively correlated with mating success for grey seals (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2004, Lidgard et al. 2012), there is still considerable variation in male reproductive success, aggressive behaviours, and timing of activities within breeding seasons that has not been examined. Therefore, the aims of this study were to explore within the Tenured male grey seal breeding strategy the role of within-season scheduling of dominance, as a proxy for reproductive effort, and assess if timing of dominance can explain some of the variation in individual mating success for male grey seals. We tested whether Tenured males who time their peak dominance to synchronize with peak female availability achieved greater mating success or if timing provided no additional benefits relative to length of stay. We predict that within the Tenured male strategy, individuals who cannot achieve the maximum durations of stay (e.g. smaller males) will time their RE early or later in the season to gain mating success. While this tactic has been suggested as a mechanism for smaller males to avoid conflict with larger males (Mysterud et al. 2008, Mason et al. 2012), we

predict that males peaking early or late in the season will engage in a greater frequency of aggressive interactions as sex-ratios during these periods are male-skewed. Further, we examined if individuals exhibited inter-annual consistency in their timing of reproductive effort to suggest the presence of alternative male mating tactics within the Tenured strategy. By assessing the consistency in male's tactics across consecutive years, this will provide initial insights into how flexible Tenured males are in their responses to intra and inter-annual changes in resource availability.

## **Methods**

### **Ethical Note**

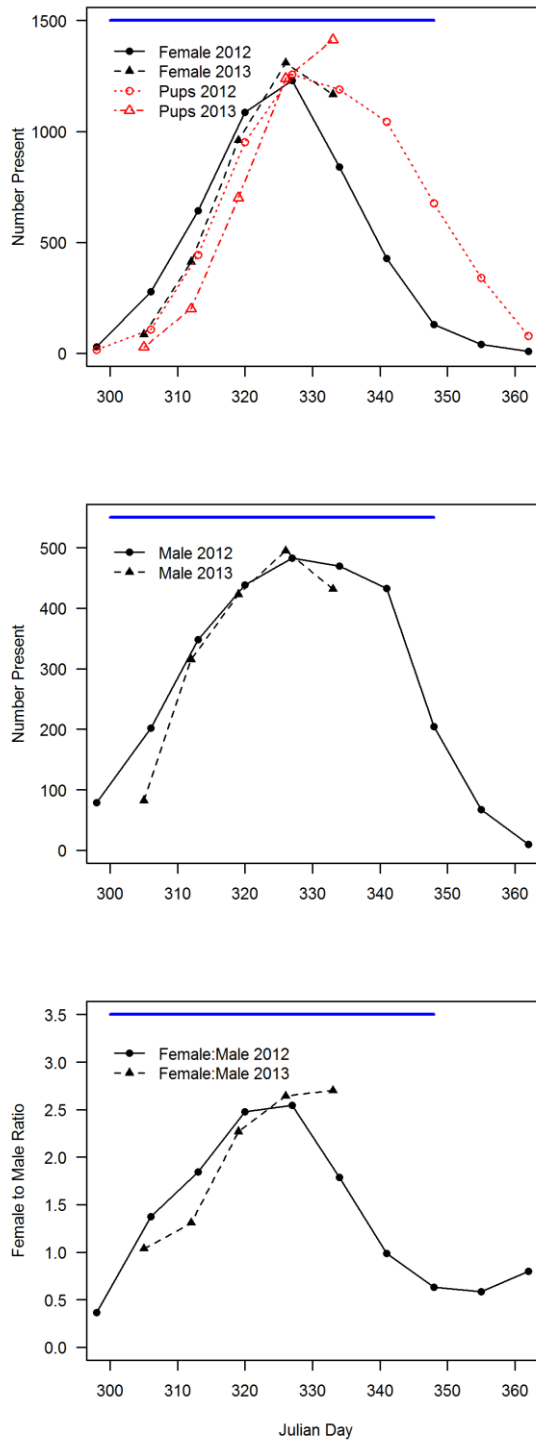
This study was observational in nature, and all work was approved by Durham University Animal Welfare Ethical Review Board and complied with ASAB ethics guidance and UK Home Office legislation.

### **Observational methods**

Fieldwork was carried out at the Donna Nook grey seal breeding colony on the mainland North Lincolnshire coast, eastern England, 53.47°N, 0.15°E (Bishop et al. 2014). The habitat at the Donna Nook colony is a mixture of shallow dunes, sand flats and marsh grass. Two main breeding aggregations of females form within the Donna Nook colony: one at the waters' edge, and one at the dune line, approximately 1 mile inland from the water's edge. All observations were conducted at the inland aggregation. The breeding season at Donna Nook spans from late October through December with peak pupping occurring around 23 November. Observations in the field were conducted 27 October -14 December 2012 (d = 49); and 27 October - 12 December 2013 (d = 47), during all available daylight hours for an average of 8h 48m of observations daily. Observations were conducted from observational hides at two locations within Donna Nook approximately 500m apart, and separated by a bend in the dune line (Hide 1: 53.474° N, 0.155° E, Hide 2: 53.476° N, 0.148° E). Two observers alternated between the two hides daily, allowing for full coverage of the site. A weekly walkthrough census was carried out in both years by the head warden from the Lincolnshire Wildlife Trust, during which the total number of adult females, adult males, and pups present were counted. Counts were used to generate

attendance pattern curves (Figure 1) that describe the relative timing of female and male attendance and pup production within and between years. Individual females remain ashore for 18-20 days, during which they give birth to a single pup, and wean the pup after approximately 18 days of nursing (Pomeroy et al. 1999b). Peak female attendance occurred on Julian Day 327 (Figure 1). Oestrus for female grey seals occurs during a very short window circa 16 days postpartum (Boness and James 1979, Pomeroy et al. 1999, Twiss et al. 2006). While the count of peak female attendance is comprised of females with pups that range in age from new-born through to almost weaned, it is evident from these attendance curves (Figure 1) that after JD 327 the number of females departing (and therefore not available for Tenured males to mate with) exceeds the number of arrivals and female attendance sharply declines, suggesting that peak female attendance is a conservative estimate of peak resource availability for Tenured males.





**Figure 1:** Weekly census counts for females and pups (a); males (b), and the female to male ratio (c) at Donna Nook in 2012-2013. Blue lines represent the extent of observations. Data past Julian Day 333 in 2013 (November 29) were not available due to atypical storm surge limiting capacity to conduct weekly counts of the entire colony. Data from: Lincolnshire Wildlife Trust

All males within the study areas were individually identified daily via pelage patterns and scars in the field (Twiss et al. 1994), or *post hoc* from high-resolution pictures taken with a Canon EOS 30D, 100–400 mm lens. Locations of all males were mapped hourly on printed aerial photos of the colony (Twiss 1991, Twiss et al. 1994, Bishop et al. 2015a, b). Incidences of aggression involving at least one identified male were recorded by the observer with notation of participants' IDs and start and end times (Bishop et al. 2015b). Aggressive interactions are attention grabbing and sufficiently rare, allowing all occurrences to be recorded while performing other observations (Altmann, 1974). Male grey seals in this study engaged in an average of 12 aggressive interactions per day ( $\pm 0.6$  se). The outcome of each interaction was noted as either a Draw or Win-Loss. A male was determined to have won an encounter if his opponent moved away or was chased away and lost his position amongst females; otherwise the aggressive interaction outcome was defined as a draw (Anderson and Fedak 1985, Twiss 1991, Twiss et al. 1998, Bishop et al. 2015b). Draws were included in this assessment because the key components of maintaining position on the colony for grey seals are winning male-male contests, and engaging in interactions that result in draws (Anderson and Fedak 1985). The average daily rate of aggression was calculated for each male (Bishop et al. 2015b). Body length is a significant predictor of mass (Twiss 1991), and was used as our proxy for male size. Photographs collected throughout the season were used to calculate multiple estimates of standard length (nose-to-tail: range 166.1–240.3 cm  $\pm$  0.5–10.9 cm SE) for each male using photogrammetry (Jacquet 2006, Bishop et al. 2015a). This method utilized established formulas describing the linear relationship of how the ratio of the known length of an object (cm) to the width of the object in a photograph (pixels) changes as distance from the camera increases (Bishop et al. 2015a). Maximum estimated standard lengths for each male were used in this analysis.

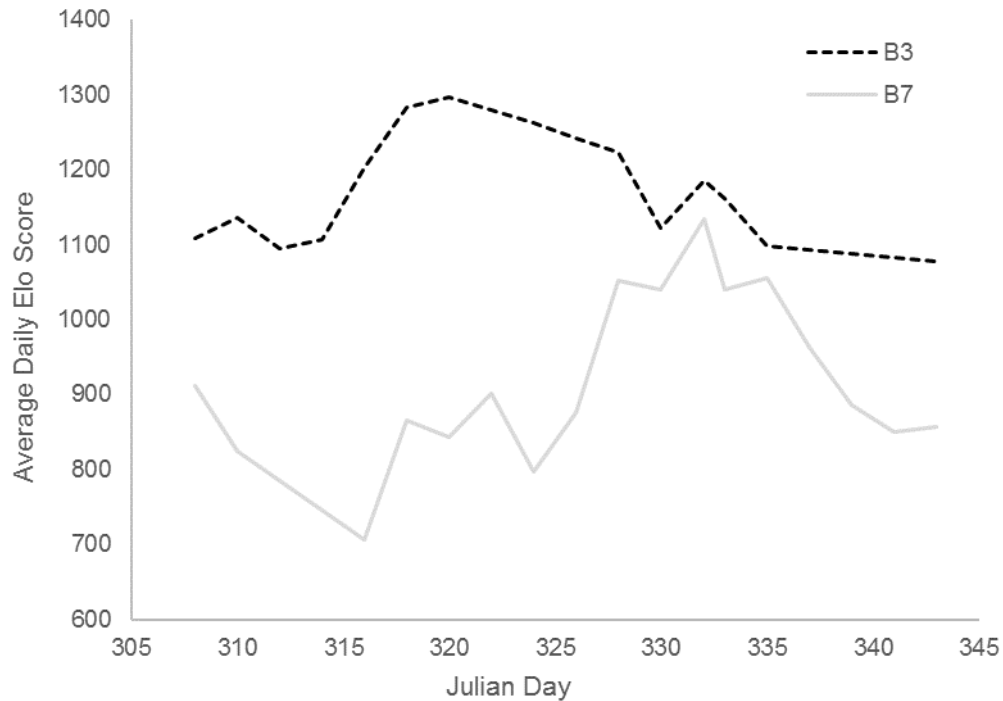
For sexual activities, each copulation event was recorded as either an attempted copulation or copulation, dependent on the absence or presence of intromission respectively. Copulations were also sub-classified into successful or unsuccessful. 'Unsuccessful' copulations, where the male achieved intromission but lost contact with the female after a short period of time due to factors such as female aggression, have been shown to last no longer than 7 min on average (average total duration of a 'successful copulation' = 20min, Twiss 1991, Twiss et al. 2006). Therefore, we conservatively defined a 'successful copulation' as a male remaining in the copulatory position for a minimum of 10 min

without disturbance. With this criterion, we observed 313 instances of intromission but omitted 37 observations where the copulation was determined to be unsuccessful. As the timing of ejaculation is unknown for this species, this definition might be underestimating individual reproductive success if ejaculation occurs immediately following intromission. However, Twiss et al. (2006) found that over 80% of assigned paternities agreed with observations of the sexual behaviour, thus suggesting our criterion provides a valid, if conservative, estimate of mating success from behavioural observations.

### **Identifying timing of Dominance: a proxy for Reproductive Effort**

For comparability with previous studies on dominance and mating success for this species only males present for  $\geq 2$ d and who participated in  $>10$  aggressive interactions were included in dominance calculations (2012  $n = 74$ , 2013  $n = 103$ ) as this ensures males were considered Tenured and engaged in a sufficient number of interactions to calculate a dominance score (Boness and James 1979, Twiss 1991, Twiss et al. 1998, Bishop et al. 2015b). Differences in the number of males between 2012 and 2013 are not a product of sampling effort, as duration and frequency of observations were identical across these years, but likely reflect different male activity patterns. We calculated dominance as an Elo score, a metric which estimates an individual's dominance along a sequence of aggressive interactions (Porschmann et al. 2010, Neumann et al. 2011). The parameters of the Elo calculations were set with a starting score of 1000 for every male and a  $k$  of 200, where  $k$  is the amount a male's score will shift with a win, loss, or draw ( $0.5 * k$ ) and is weighted by the score of his opponent (Neumann et al. 2011). The constant  $k$  can be set at any value between 16-200 (Neumann et al. 2011). Since not losing is key for mating success and dominance for grey seals (Anderson and Fedak 1985), we set  $k$  to maximise the penalty for losing. Elo scores were updated following every aggressive interaction with another known male. In the UK, tenured male grey seals that return to breed across multiple years exhibit site fidelity and males do not shift in average dominance scores substantially between years (Twiss 1991, Twiss et al. 1994). Therefore, we based Elo calculation on a continuous consecutive assessment across all years males were observed to take into account previous season's reproductive success (Neumann et al. 2011). To confirm that this did not disadvantage males starting with lower scores in their second year, we calculated the mean Elo score for individuals in each season separately and found the difference in the two calculations was an average of 18.75 (3.6% of total range). Scores were averaged daily (Figure 2)

and the date on which the average score was greatest within a breeding season was used as our metric for timing of high dominance: Peak Elo Day.



**Figure 2:** Examples of two males’ dominance patterns within a breeding season; points represent the males’ average Elo score on a given day. “B3” peaked in dominance on Julian Day 320 after which his score gradually declined, whereas “B7” started with a low Elo score, and then surged and peaked on Julian Day 332.

### Statistical Analyses

We first assessed if timing of peak dominance or duration of stay for male grey seals was associated with specific size-classes or was a mechanism for conflict-reduction (Mason et al. 2012). Our prediction was that males timing reproductive effort before or after peak female attendance would be smaller, but both early and late males would have a higher average number of aggressive interactions per day as at the start and end of the season there are relatively more males per female (Figure 1, Boness et al. 1995) and social structures are less stable (Bishop et al. 2015b). We used generalized linear mixed-effects models, GLMMs, with Poisson distributions (link=log) to test if males’ estimated body length and average number of aggressive interactions per day were predictors of timing of peak dominance

(response variable = Peak Elo Day relative to date of peak female attendance on the colony), or duration of stay (response variable = total number of days observed). Male ID and year were included as random effects to account for pseudoreplication and observations within years being correlated ( $n = 150$  records with standard length estimates, 127 IDs, 2 Years). These models were fit using R package {lmer4}.

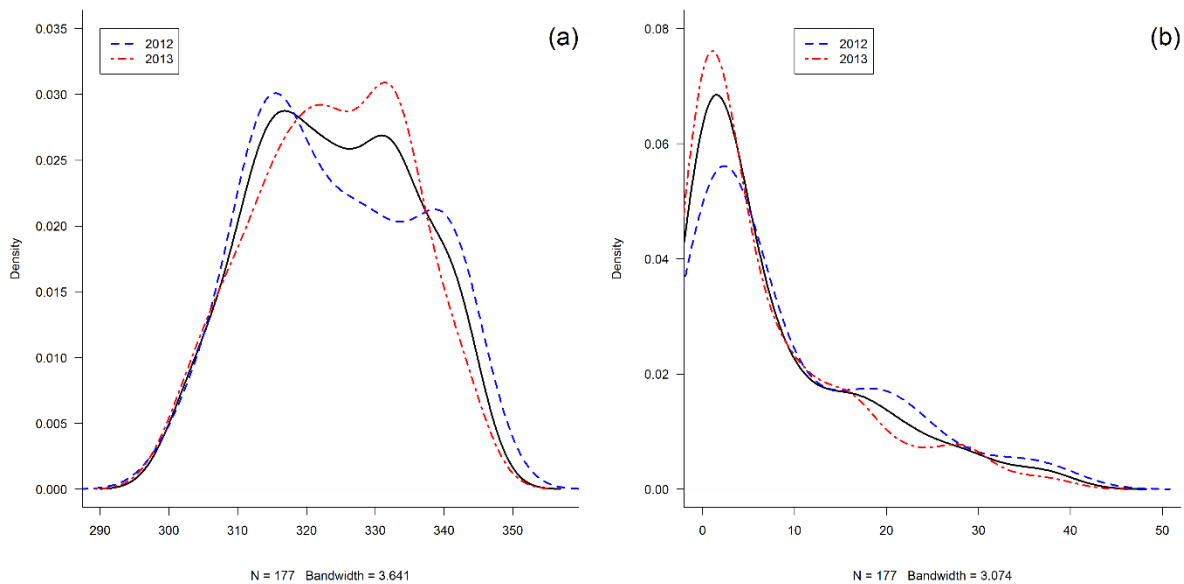
We then examined how timing of reproductive effort (via peak dominance) and duration of stay contributed to the variation in observed mating success for Tenured males by fitting a generalized additive mixed effects model (GAMM) with Poisson distribution that included Male ID and Year as random effects to account for individuals present in multiple years and interannual variation ( $n = 177$  observations, 153 IDs, 2 Years). These models were fit using R package {gamm4}. We chose to use a GAMM as we predicted mating success would have a non-linear relationship with timing of peak dominance, and GAMMs allow for fitting a mixture of linear and smoothed relationships. Our response variable was the number of observed successful copulations, and predictor variables were all initially set as smoothed-term factors: timing of peak dominance (Peak Elo Day), intensity of dominance (dominance rank based on relative Elo score achieved on Peak Elo Day) and duration of stay (total number of days observed on the colony). If the model output indicated that the estimated degree of freedom for one of the covariates was 1.00 then the smoother function for that covariate was replaced as a linear term (Ingram et al. 2007). Arrival date was considered for inclusion in the model but it shared a positive co-linearity with length of stay and was therefore omitted. Our model selection criteria incorporated  $AIC_C$ , a bias-corrected version of Akaike's Information Criterion that accounts for small sample sizes. We use  $\Delta AIC$  to denote the difference between the  $AIC_C$  values of each model relative to the lowest  $AIC_C$  value calculated, such that the 'best'  $AIC_C$  model has  $\Delta AIC = 0$ . Our final model set included those models with  $\Delta AIC < 6$  that were not nested versions of simpler models. These criteria prevent the selection of overly complex models (Richards 2008).

There were 24 Tenured males who were seen in both 2012 and 2013. To examine inter-annual consistency in dominance partitioning and duration, males present across both breeding seasons were examined for repeatability across years. Spearman's correlations between 2012 and 2013 were calculated for Length of Stay, Arrival Date and Peak Elo Day.

## Results

### Male timing of dominance and length of stay

Timing of peak male dominance score ranged from Julian Day 301 (October 28th) to 346 (December 12th), (median = 323) and appeared to have a bimodal distribution with greatest frequency of peaking at Julian Day 315, and then a secondary peak at Julian Day 330 (Fig.3a). On average, males peaked in dominance  $7.8 \text{ days} \pm 0.7\text{SE}$  after arrival (range 0-39) (Fig.3b). Males stayed on the colony for a mean of  $8.7 \text{ days} \pm 0.5\text{SE}$  (range 2-29).



**Figure 3:** Kernel density plot representing the distribution of the date of peak Elo score (a) and of the number of days after arrival individuals peaked in dominance (b), across both years and all Tenured males combined (solid black line). Density for 2012 (n=74) and 2013 (n=103) are shown as blue and red lines respectively. Bandwidth represents the standard deviation of the smoothing kernel.

Both size and aggression were retained as predictors of a male's total length of stay (Table 1). Larger males stayed on the colony for longer and males with a greater average number of aggressive interactions per day stayed on the colony for a shorter duration (Table 1). Size and aggression were not significant predictors of timing of peak dominance (Table 1).

**Table 1:** Effect size (standard error), AIC<sub>c</sub>, ΔAIC, and model weight from GLMMs predicting Peak Elo Day (relative to peak female attendance, Julian Day 327) and length of stay on the colony. The null model was best for predicting Peak Elo Day and the full model was best under selection criteria for predicting days on colony. All models included male ID and year as random effects, (n = 150 observations, 127 IDs, 2 Years).

Response	Model	SL (se)	DAI (se)	AIC <sub>c</sub>	ΔAIC	weight
Peak Elo Day (relative to peak female attendance)	Null			1030.3	0	0.412
	1a	-0.0041 (0.0035)		1031.0	0.74	0.285
	1b		-0.0054 (0.0078)	1034.1	1.63	0.182
	Full	-0.0040 (0.0035)	-0.0050 (0.0077)	1037.1	2.47	0.120
Days on Colony	Full	0.018 (0.003)	-0.030 (0.007)	970.7	0	0.999
	1a	0.017 (0.003)		984.4	13.6	0.001
	1b		-0.027 (0.007)	992.8	22.0	0
	Null			1002.5	31.8	0

SL= estimated maximum standard length, DAI = Average number of aggressive interactions per day, se = standard error

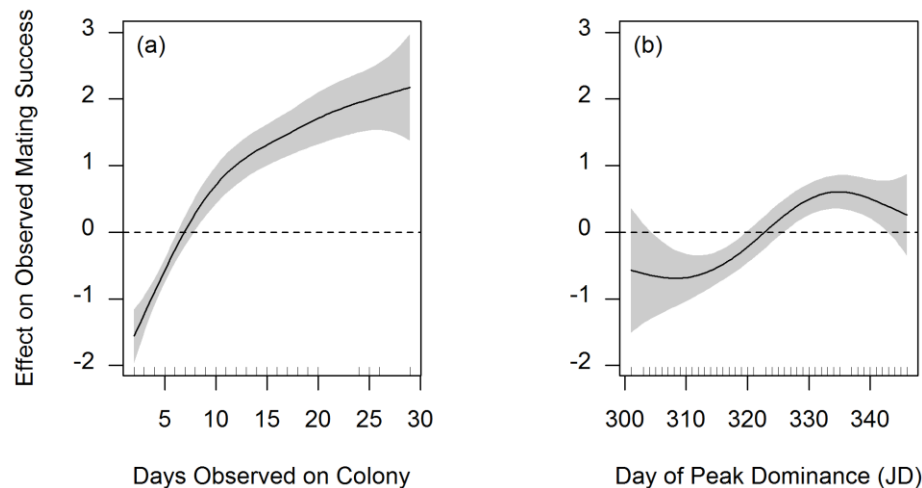
### Mating success

Average male mating success was  $1.56 \pm 0.2$  SE (range = 0-14). Length of stay and timing of peak dominance were both retained as non-linear predictors of observed mating success (Table 2, Figure 4a). Intensity, the relative dominance rank achieved on day of peak Elo, had an estimated degree of freedom of one in the full model. All models were re-run with this factor as a linear term but this did not improve model performance and intensity was not retained. From the visualization of the smoothed relationship between observed mating success and length of stay (Figure 4a), length of stay had an initial positive relationship with observed mating success, but this effect became weaker for stays longer than 10 days (Fig. 4a). Timing of peak dominance also shared a general trend of a positive relationship with observed mating success (Figure 4b). Males peaking between Julian Day 308-318 (November 4-14) had lower than average mating success, while males peaking between Julian Day 326-342 (November 22-December 8) had greater than average mating success (Fig.4b).

**Table 2:** Estimated degrees of freedom (smoothed-terms (s)), estimate and standard error (linear-terms), AIC<sub>c</sub>, ΔAIC, weight, and R-squared (R-sq) from the GAMMs predicting observed mating success. The

model with cubic splines of Peak Elo Day and Days on Colony was best under our selection criteria of a model having a  $\Delta AIC < 6$  and not being a more complicated version of a nested model (Richards 2008). All models included male ID and year as random effects ( $n = 177$  observations, 153 IDs, 2 Years).

Model	s(Peak Elo Day)	s(Days on Colony)	Intensity	AIC <sub>c</sub>	$\Delta AIC$	weight	R-sq
	Estimated Degrees of Freedom		Estimate (se)				
1a	3.085	3.041		476.9	0.0	0.867	0.541
Full	3.179	2.959	-0.02 (0.02)	480.6	3.8	0.133	0.537
1b		3.296		494.6	9.1	0.000	0.447
1c		3.298	0.01 (0.02)	498.7	12.9	0.000	0.441
Null				626.2	149.4	0.000	-



**Figure 4:** Estimated smoothing curves for GAMM describing the effect (a) Duration of Stay on the Colony and (b) Timing of Peak Dominance (JD = Julian Day) have on observed mating success. The solid black line indicates the smoothing curve, while the grey shaded area represent the approximate 95% confidence intervals. On the y-axis, 0 corresponds to no effect of the covariate, values  $>0$  indicate positive correlation and values  $<0$  indicate negative correlation. The effect, relative to the mean mating success (dashed line), for a particular value of a covariate can be obtained as the natural anti-logarithm of the corresponding y-axis value (solid black line).

#### Consistency of individual's tactics



For the 24 males seen in both seasons, there was no consistency in timing of peak dominance (*Spearman's Rank Correlation*  $r = 0.16$ ,  $df = 22$ ,  $P = 0.46$ ), date of arrival (*Spearman's Rank Correlation*  $r = 0.226$ ,  $df = 22$ ,  $P = 0.2865$ ) or length of stay (*Spearman's Rank Correlation*  $r = -0.09$ ,  $df = 22$ ,  $P = 0.66$ ) between 2012 and 2013.

## Discussion

Timing of reproductive effort and its effect on mating success has been examined in several species (Myserud et al. 2008, Mason et al. 2012, Parker and Maniscalco 2014), but for species where handling or repeat captures are difficult, assessments of within-season individual variation of timing of reproductive effort have been limited. Additionally, prior to this study the general characteristic of Tenure for grey seals has been that longer stays are positively associated with greater mating success (Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2004, Lidgard et al. 2012). By using intraseasonal variation in dominance as our proxy for reproductive effort, we refine this understanding and show using observational methods that within the generalized strategy of "Tenure", males that timed their reproductive effort during or after peak female attendance had increased mating success, and that timing reproductive effort later in the season resulted in more success than exerting high reproductive effort early in the season. We found that larger males stayed longer and males with greater rates of aggression had shorter stays, but contrary to our prediction, there was no evidence to suggest that timing reproductive effort early or later in the season was associated with smaller males or greater rates of aggressive interactions. Timing of reproductive effort for individuals was also not consistent across the two years of the study, suggesting there may be individual behavioural flexibility or that males might respond to shifts in localized conditions.

Assessing differences in attendance duration and timing of reproductive effort across individuals enabled us to first examine if there were any patterns to the types of males exhibiting specific temporal or attendance tactics. Our results indicated that individuals with greater size and fewer aggressive interactions had longer lengths of stay. This matches previous work that has shown that, for many polygynous species, the total energy available for fasting and the adoption of mechanisms that reduce energetic expenditure are positively associated with mating success (Clutton-Brock and Albon

1979, Anderson and Fedak 1985, Twiss 1991, Lidgard et al. 2001, McElligott et al. 2001, Lidgard et al. 2004, Twiss et al. 2006, Pörschmann et al. 2010, Crocker et al. 2012, Lidgard et al. 2012, Meise et al. 2014). With regards to timing however, we found no evidence to suggest size or rates of aggression were predictive of male timing of reproductive effort. Late timing of reproductive effort has been considered a conditional tactic that young or smaller individuals use to avoid costly interactions with other larger males (Gross 1996, Mysterud et al. 2008, Mason et al. 2012), but may result in a greater number of aggressive interactions between similar size/age class individuals as male-female sex ratios draw closer to equivalent (Boness et al. 1995, Twiss et al. 1998). It is possible we did not capture this shift in size or aggression in our sampling window as our observations concluded approximately 15-20 days before all males had left the colony. However, our study captured the majority of the female attendance duration and the associated decline in female:male ratios late in the season as females departed, which is when we would have expected to see shifts in aggression (Fig 1). Future work targeting this late period could help clarify the apparent absence in size-related associations with timing of reproductive effort and would also provide the opportunity to look for other alternative tactics that could be linked to timing of reproductive effort, such as inter-colony dispersal (Robertson et al. 2006). For male grey seals, inter-colony movements are possible due to differences in breeding timing across the UK (Coulson 1981) and could be tracked via observational methods and photo-ID networks (Hiby et al. 2012, Patterson et al. 2013).

We found mating success had positive relationships with both duration of stay and timing of reproductive effort. In contrast to previous work which suggested a linear relationship between male duration of stay and mating success (Twiss 1991), we found that the relationship between length of stay and mating success was non-linear, with a stronger effect when increasing tenure from 2-10 days, followed by a reduced effect when males stayed for longer than 10 days. Winning, or more precisely not losing, aggressive interactions is required to establish and maintain a position amongst females, and increases an individual's dominance score (Anderson and Fedak 1985, Twiss et al. 1998), but maintaining access to females can be costly in terms of metabolism (Copeland et al. 2011), stress (Lidgard et al. 2008) or physical injury. Donna Nook is characterized by relatively high individual rates of aggression and closer male-male proximity than observed on off-shore UK colonies such as North

Rona (Twiss 1991, Bishop et al. 2015b). This may explain the discrepancy between previous findings of a linear relationship between length of stay and mating success and the findings of the present study. Our findings could suggest that at Donna Nook, the costs and risks associated with increased aggression would be worthwhile early in a males' tenure on the colony as the marginal benefits of mating increase substantially for each day longer they can remain. Then, as marginal benefits diminish with increasing length of stay, other mechanisms might become more important to facilitate conservation of energy instead of risky behaviours that could result in losing position. For example, it has been shown that males which maintained local social stability through engaging in low-cost threat behaviours with neighbours had fewer daily aggressive interactions on average, but that dominance score shared no relationship with rate of aggression (Bishop et al. 2015b). In the present study, we found that males with lower rates of aggression stayed longer, and length of stay positively predicted mating success. Therefore, winning or maximizing dominance score is not the key driver in this system, but how individuals achieve a balance in the trade-off between behaviours and energetics (fighting and fasting) within a breeding season is important to consider in terms of predicting male fitness. It will be informative for future work to examine of how differences in colony dynamics, topography, and demography influence this apparent trade-off between aggression and fasting within breeding seasons.

Timing of peak dominance did share a relationship with mating success, with males peaking in reproductive effort just before or during peak female attendance achieving a greater number of observed copulations. A similar pattern has been observed for Steller sea lions (*Eumetopias jubatus*). Males in centrally located territories, who maintained positions throughout female pupping had the greatest relative mating success across years, but males that held sub-optimal territories and timed their arrival to just prior to peak female attendance still achieved some mating success (Parker and Maniscalco 2014). In the present study, males who peaked in their reproductive effort early had poor mating success. This finding is somewhat in contrast to other systems with spatially and temporally constrained breeding seasons where early arrival and territory establishment is often associated with greater reproductive fitness (Pomeroy et al. 1999, Smith and Moore 2005, Cordes and Thompson 2013). Some early breeding female phocid seals have greater reproductive investment in their offspring and greater fitness than later arrivals at breeding colonies (Boness et al. 1995, Cordes and Thompson 2013). We found a relatively

low number of copulations associated with the tactic of peaking early, so while males that express high reproductive effort early might be targeting higher quality females, without a moderate length of stay they could be experiencing greater risks of losing access to females before any mating success is achieved.

Interannual variability in female arrival and reproductive phenology could further increase the risks of early reproductive effort tactics if males experience temporal mismatch between timing their reproductive effort and availability of their resource, oestrus females (Crick et al. 1997, Forrest and Miller-Rushing 2010, Cordes and Thompson 2013). Nesting date for birds in the UK (Crick et al. 1997), ringing date for seabirds (Møller et al. 2006), and pupping date for harbour seals, *Phoca vitulina*, (Cordes and Thompson 2013) have shown advances over time which can be attributed to various factors such as climate change, the North Atlantic Oscillation, or population density respectively. In our study, female attendance and pup production in 2013 was approximately 5-7 days later than observed in 2012. When species are exposed to variable environments, alternative mating tactics enable males to maintain high levels of fitness across unpredictable fluctuations (Gross 1996, Meise et al. 2014). Populations able to cope with disturbances are those that contain some portion of behaviourally flexible individuals and such inter-individual variation can have profound consequences for how populations respond to stress (Bolnick et al. 2003, Araújo et al. 2011, Carrete and Tella 2011, Violle et al. 2012). Across our two study years, male grey seals did not appear to be consistent in their tactic in regards to arrival, peak reproductive effort, or duration of stay; which could suggest their behavioural mechanisms for optimizing mating success are reactive to local current conditions. Longitudinal data over a much longer time period would be necessary to confirm if the differences we observed in individual, interannual patterns of reproductive effort are in response to natural fluctuations in weather (Meise et al. 2014) and phenological shifts in resources and mates (Forrest and Miller-Rushing 2010), or if any individuals within the population are fixed in their behavioural tactics within the Tenured strategy (Twiss et al. 2012).

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